

Mortality of *Anaea ryphea* (Lepidoptera: Nymphalidae) Immatures in Panama

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Abstract. In order to assess the main mortality factors acting on immature stages of *Anaea ryphea* in Panama, I censused a population of this butterfly weekly from August 1991 to May 1992. A total of 515 eggs found on 129 marked food plants were individually numbered and followed through larval instars until death or disappearance. Results suggest that egg predation and rainfall are the main factors responsible for the low level of first instar recruitment. Egg parasitism rate was considered high for a tropical insect population, although it accounted little for overall mortality. A vertical life table constructed with data from one generation showed mortality was similar among larval instars, but was significantly higher for the eggs. No larval parasitism was observed, a finding perhaps related to low larval densities at the site.

KEY WORDS: abundance; *Anaea ryphea*; life table; regulation; parasitism; tropics.

INTRODUCTION

One of the most interesting issues in Population Ecology involves the mechanisms responsible for keeping population densities within certain limits, below their theoretical carrying capacities, as predicted by exponential models. Many factors can act together to reduce levels of reproduction and survivorship when density increases. The effect is said to be density-dependent, and these factors are said to be the population regulators (Lack 1954; Solomon 1964; Begon and Mortimer 1986) — although Wolda (1989b) states that there are no studies showing that density dependent processes definitely do act on natural populations in such a way as to keep numbers within stable limits.

It was believed that tropical insect populations should be less variable in numbers than those of temperate areas, both seasonally and between years (Andrewartha and Birch 1954; Solomon 1964; Pianka 1970), due to the assumed stability of tropical environments. Studies carried out later showed that tropical insect populations not only can be very stable in numbers (Ehrlich and Gilbert 1973) but some times are subject to fluctuations, outbreaks and variations in abundance similar to those that occur in temperate areas (Wolda and Foster 1978; Wolda 1983, 1989a; 1992 a,b). Even in tropical environments considered to be aseasonal, there is seasonality in insect phenology (McElravy *et al.* 1982; Wolda and

Flowers 1985), and one wonders what factors could be responsible for this phenomenon. It is known that, among others, thermoperiodism can influence growth rates (Beck 1983) and that photoperiodism plays an important role in the reproductive diapause of certain species of butterflies (Riley 1988), sometimes causing seasonality in their adult occurrence pattern.

Studies involving population variations in tropical insects, apart from analyzing reproduction, are also very concerned with mortality levels. Life tables are constructed to evaluate these parameters (Royama 1981; Stiling 1988; Hassell *et al.* 1989). Climatic and environmental factors, natural enemies, and competition are usually considered the main sources of mortality, but Crawley (1989) pointed out that outbreaks of herbivorous insects occurring soon after the use of broad spectrum insecticides suggest that their populations, when in low densities, are regulated by natural enemies alone. Natural enemies and competition for common resources are usually regulating factors, related to density (Nicholson 1933; Lack 1954; Eberhardt 1970; Lance *et al.* 1987).

Because there are very few studies that analyze mortality factors in natural tropical insect populations, especially in folivorous species, the aim of this study was to characterize the main sources of mortality acting on immature stages of the butterfly *Anaea ryphea* Cramer 1775 (Nymphalidae: Charaxinae) in Panama, including comments on its life cycle.

PROCEDURES

Study site

The study site was a small forested area along the road leading to Galeta Island, Colón Province, on the Caribbean (north) coast of the Republic of Panama, east of the Panama Canal. The site is located at sea level, and the annual average temperature is around 28°C. Average rainfall at Galeta Island is 2,500 mm, the same value registered for Barro Colorado Island, which is located close by to the south. A dry season occurs, usually from December through April. The study area was chosen because it had 129 individuals of *Croton billbergianus* (Euphorbiaceae), the main larval foodplant of *A. ryphea* in Panama (personal observation). This number was considered suitable for my study.

Data collection

I labelled all 129 plants with plastic tags, and made a weekly census from August 1991 to May 1992. Every leaf of each plant was checked, and eggs were numbered individually with a plastic band tied to the petiole of the leaf on which each was found. This method enabled me to identify each one of them, because there is usually but one egg or larva per leaf (Caldas 1994). I followed all of them until disappearance or death, and, depending upon age class, attributed different sources of mortality to each one. Predation was considered a source of mortality when no other

apparent reason could be found, as is usually done in studies of this kind. Rainfall was not included as a source of egg mortality because eggs were not washed away after strong storms (personal observation). When egg frequency increased I began to visit the area at shorter intervals, and by November I was going there almost every other day.

In addition to field observations, 40 eggs were taken to the laboratory and reared under constant temperature (16-18° C) and relative humidity (60-65%), in order to obtain information on life cycle.

RESULTS AND DISCUSSION

Variation in abundance of *A. ryphea* larvae is shown in Figure 1. The pattern observed in the figure suggests that there was only one generation of significant size in the area during the study. *A. ryphea* larvae were not observed until early August, well after the beginning of the rainy season (late April). A significant number of eggs ($n > 5$) was reached only in October. From then on, the larval population increased without a clear peak, and the number of individuals remained around thirty. In mid-December, when the population was decreasing, most of the plants were partially cut, without warning, in a road-side cleaning operation by the US Navy, and from then on no new larvae or eggs were found on the remaining leaves.

Rainfall was relatively constant, high and regular, between August and November, decreasing from December on, when dry season began. Rainfall was low throughout the rest of the study. Figure 2 shows a climograph for the area with a hypothetical constant temperature of 28°C — no temperature data were available due to equipment problems, but judging from data taken at La Galeta in previous years (Cubit *et al.* 1988) temperature at that area hardly varies. The main seasonality factor seems to be rainfall, which was unusually low during December 1991 and January/February 1992 (Windsor *et al.* 1990; D. Windsor, personal communication).

Rainfall pattern probably had a great influence on this population. I observed that strong rains kill young (mainly first instar, a few second instar) larvae (Caldas 1994). They also probably hinder oviposition (Ehrlich 1984). Recruitment of first instars was very low, in spite of continuous oviposition, because newly eclosed larvae were washed away easily from their perches on the midvein. Because rains were very strong and frequent (almost daily) at the site, this factor probably was very important in determining population numbers. Toward the end of the rainy season — in October, when rainfall subsided a little — the population was able to increase, but not very much, because strong rains began again. The population was thus prevented from reaching a peak until the abrupt start of dry season in December, at which time the bushes were cut. These two factors could have determined the end of the reproductive season, and population declined.

Of the 515 eggs marked, 85% disappeared, and parasitism by

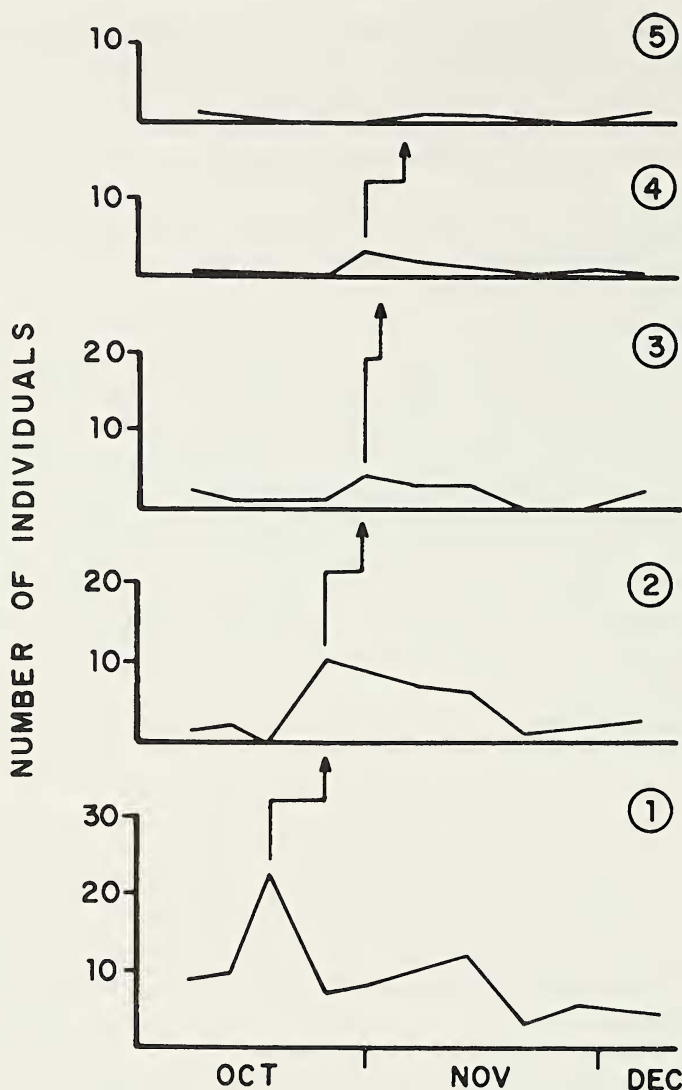


Figure 1. Total number of *Anaea ryphea* larvae (per instar) censused in Panama during the period of study. Arrows show the advance of a cohort through time.

Trichogramma sp. (Trichogrammatidae) was registered in 28% of the ones that remained in the field (Table 1). The evaluation of parasitism as a mortality factor can be particularly difficult if hosts cannot be identified individually (Hassell and Waage 1984). Overestimation of parasitism levels is common, because the remains of attacked individuals persist longer in the population. In this study all hosts were individually numbered, thus avoiding overestimation of egg parasitism. Still, the percentage found is considered high for a insect population. Courtney

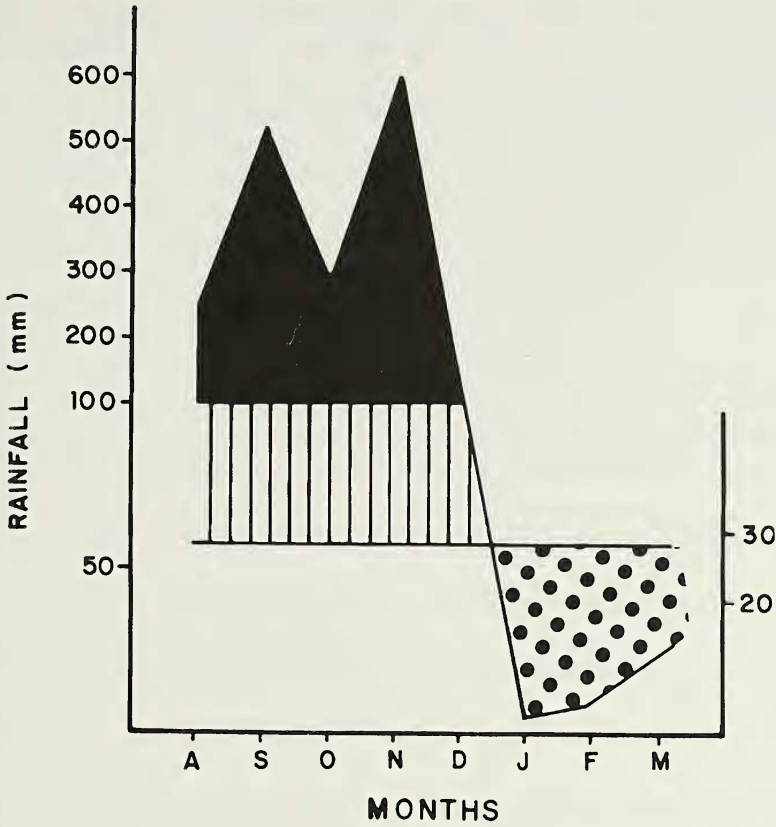


Figure 2. Climograph for the period of study in Panama; temperature is hypothetical (see text for details). Dotted area, dry period; lines, wet period; black, super-wet period.

and Duggan (1983) considered egg parasitism an important source of mortality, but pointed to the number of eggs laid by females as the key-factor for *Anthocaris cardamines* (Lepidoptera: Pieridae). Warren *et al.* (1986) say that egg parasitism by trichogrammatid wasps was always below 20% during their 5 years of study of *Leptidea sinapis* (Lepidoptera: Pieridae); the same thing happened with *Ladoga camilla* (Lepidoptera: Nymphalidae) in England (Pollard 1979). No density dependence was found in his study, although weather conditions were considered determinants of density. In a population of *Epiphyas postvittana* (Lepidoptera: Tortricidae) in Australia, parasitism was considered insignificant compared to predation on eggs over sixteen generations (Danthanarayana 1983), a situation which seems to be similar to the one found for *A. ryphea* during this season in Panama. The high rate of egg disappearance attributed to predation seemed to have a much stronger impact on the *A. ryphea* population than did parasitism. The percentage of egg parasitism was even higher for the eggs reared in the laboratory (see below), although the low number of eggs in the rearing experiment

Table 1. *Anaea ryphea* egg survivorship in Panama (actual values; * = total k value for eggs).

Total(N)	"Dead"	Mortality Factor	log N	k
515			2.711	
	437	disappearing		0.819
78			1.892	
	22	parasitism		0.144
56			1.748	
	5	non fertile		0.041
51			1.707	
				1.004*

Table 2. Vertical life table for *Anaea ryphea* during the period of study in Panama (* = total value for k; 1S, first instar; 2S, second instar; etc.).

X	Total(N)	"dead"	Main Mortality Factor	log N _x	k _x
Egg	515			2.711	
		422	multiple		0.743
1S	93			1.968	
		52	Rainfall		0.355
2S	41			1.613	
		24	Predation/rainfall		0.383
3S	17			1.230	
		9	Predation		0.327
4S	8			0.903	
		4	Predation		0.301
5S	4			0.602	
					2.109*

does not allow it to be conclusive. The low density of larvae at the study site might be responsible for the apparent absence of larval parasitoids.

The life table shows high mortality for all instars (Table 2), although different sources are likely to be acting on each one of them. Thus, apart from parasitism and predation on eggs, predation by invertebrates (mainly ants and wasps) could be high for small larvae. Predation by vertebrates could be an important mortality factor also for large larvae, although the effect of rainfall cannot be discarded. The fact that mortality of *A. ryphea* third and fourth instars by rainfall has not been largely observed in the field at Campinas during 3 years of study (Caldas 1994) leads me to infer predation as the main mortality factor for these instars in Panama. Predators should be extremely efficient at predating *A. ryphea* larvae and eggs — hence the attribution of "predation" as the main mortality factor for third and fourth instars in the life table. No other explanation for the disappearance could be found, and it is common

to attribute it to predation, because it is very difficult to observe in the field (Pollard 1979; Courtney and Duggan 1983).

Two species of Ponerinae ants were observed frequently; one of them was described as interacting with Riodinidae larvae (DeVries 1988, 1991; DeVries and Baker 1989). Possibly these ants or other insects attracted to the extrafloral nectaries of *C. billbergianus* could be predators on larvae, or could be defending the plants against herbivory in the same way described by Tilman (1978) in cherry plants. This kind of interaction is not uncommon, and its role on herbivory reduction has been analyzed in various ways (Bentley 1976; Oliveira *et al.* 1987).

Fifteen (37.5%) of the forty eggs taken to the laboratory were parasitized by *Trichogramma* sp., and 2 were non-fertile. First instar larvae eclosed from the remaining 23 eggs 5 to 6 days later. Under constant conditions, the average time for the life cycle to be completed was 83.7 days (standard deviation 8.8 days). Individuals were smaller than the ones found in the field, and had the following characteristics:

First instar: maximum length 5 mm, first stadium average duration: 9 days (n=18).

Second instar: maximum length 9 mm, second stadium average duration: 7 days (n=17).

Third instar: maximum length 15 mm, third stadium average duration: 9 days (n=15).

Fourth instar: maximum length 19 mm, fourth stadium average duration: 13 days (n=14).

Fifth instar: maximum length 29 mm, fifth stadium average duration: 23 days (n=13).

Pre-pupa: maximum diameter 14 mm, prepupal average duration: 2.5 days (n=13).

Pupa: maximum length 13 mm, maximum width 10 mm, pupation average duration: 20 days (n=10).

The life cycle under these conditions is longer than the 50-60 days estimated for the same species in the field at Campinas, Brazil (Caldas 1994). Given that there is an inverse relationship between temperature and developing time for insects (Southwood 1978), it is likely that the rearing temperature (8-10°C under the average outdoor temperature) was responsible for the longer development times. The sex-ratio was 2:1 (15 females to 8 males), not significantly different from unity.

Considering that *A. ryphaea* is a tropical butterfly with a probable seasonal pattern of appearance at Galeta, the question remains whether the low density observed could be considered the "lower limit" for this species. It seems reasonable to think that the ready availability of food (the food plants remain in the area after the road cleaning operation, but population did not increase again), together with climatic conditions, would favor an increase of this population, were there not mortality and immigration. The high oviposition rate observed at the site during the short period of study is a good sign of the response of females to this

conjunction of factors. I suspect that both the amplitude and seasonality of abundance of *A. ryphea* change over the years as has been observed in other insect species of nearby areas (Wolda 1992b). Predation on eggs and mechanical mortality of first instar larvae, in extremely heavy rains, could act together in a density independent way to prevent a higher level of recruitment. In any case, it could hardly be said that stable limits exist for the maintenance of this species in those areas, or that there is any sort of regulating mechanism acting in a density dependent way. As for this tropical area having environmental stability, it could be said that, apart from almost constant temperature, one cannot identify anything stable except predictably heavy rainfall. Catastrophic mortality is likely to occur everyday, but can this be considered a sign of stability? Not likely, given that the level of mortality caused by rainfall is not deterministic; it depends on a series of circumstantial factors, such as the position of the larva, the position of the leaf on which the larva is resting, the location of the plant itself, and so on.

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LITERATURE CITED

- ANDREWARTHA, H.G. & L.C. BIRCH. 1954. The distribution and abundance of animals. Univ. of Chicago Press, Chicago.
- BECK, S.D. 1983. Insect thermoperiodism. *Ann. Rev. Entomol.* 28: 91-108.
- BEGON, M. & M. MORTIMER. 1986. *Population Ecology: a unified study of animals and plants*. Blackwell, Oxford.
- BENTLEY, B.L. 1976. Plants bearing extrafloral nectaries and associated ant community: Interhabitat differences in the reduction of herbivore damage. *Ecology* 57: 815-820.
- CALDAS, A. 1994. Biology of *Anaea ryphea* (Nymphalidae) in Campinas, Brazil. *J. Lepid. Soc.* 48(3) (in press)
- COURTNEY, S.P. & A.E. DUGGAN. 1983. The population biology of the Orange Tip butterfly *Anthocaris cardamines* in Britain. *Ecol. Entomol.* 8: 271-281.
- CRAWLEY, M.J. 1989. Insect herbivores and plant population dynamics. *Ann. Rev. Entomol.* 34: 531-564.
- CUBIT, J.D.; R.C. THOMPSON; H.M. CAFFEY; & D.M. WINDSOR. 1988. *Hydrographic and Meteorological Studies of a Caribbean Fringing Reef at Punta Galeta, Panama: Hourly and Daily Variations for 1977-1985*. Smithsonian Institution Press, Washington, D.C.
- DANTHANARAYANA, W. 1983. Population ecology of the light brown apple moth, *Epyphias postvittana* (Lepidoptera: Tortricidae). *J. Anim. Ecol.* 52: 1-33.
- DEVRIES, P.J. 1988. The larval ant organs of *Thisbe irenea* (Lepidoptera: Riodinidae) and their effects upon attending ants. *Zool. J. Linn. Soc.* 94: 379-393.
- 1991. Mutualism between *Thisbe irenea* butterflies and ants, and the role

- of ant ecology in the evolution of larval-ant associations. *Biol. J. Linn. Soc.* 43: 179-195.
- DEVRIES, P.J. & I. BAKER. 1989. Butterfly exploitation of an ant-plant mutualism: adding insult to herbivory. *J. New York Entomol. Soc.* 97: 332-340.
- EBERHARDT, L.L. 1970. Correlation, regression and density dependence. *Ecology* 51: 306-310.
- EHRLICH, P.R. 1984. The structure and dynamics of butterfly populations. 25-40. In R.I. Vane-Wright and P.R. Ackery (eds) *The biology of butterflies*. Academic Press, London.
- EHRLICH, P.R. & L.E. GILBERT. 1973. Population structure and dynamics of the tropical butterfly *Heliconius ethilla*. *Biotropica* 5: 69-82.
- HASSEL, M.P., J. LATTO & R.M. MAY. 1989. Seeing the wood for the trees: detecting density-dependence from existing life-table studies. *J. Anim. Ecol.* 58: 883-892.
- HASSEL, M.P. & J.K. WAAGE. 1984. Host-parasitoid population interactions. *Ann. Rev. Entomol.* 29: 89-114.
- LACK, D. 1954. *The natural regulation of animal numbers*. Oxford Univ. Press, London.
- LANCE, D.R., J.S. ELKINTON & C.P. SCHWALBE. 1987. Behaviour of late-instar gypsy moth larvae in high and low density populations. *Ecol. Entomol.* 12: 267-273.
- MC ELRAVY, E.P., H. WOLDA & V.H. RESH. 1982. Seasonality and annual variability of caddisfly adults (Trichoptera) in a "non-seasonal" tropical environment. *Archiv. fur Hydrobiologie* 94: 302-317.
- NICHOLSON, A.J. 1933. The balance of animal populations. *J. Anim. Ecol.* 2: 132-178.
- OLIVEIRA, P.S., A.F. DA SILVA & A.B. MARTINS. 1987. Ant foraging on extrafloral nectaries of *Qualea grandiflora* (Vochysiaceae) in cerrado vegetation: ants as potential anti-herbivore agents. *Oecologia* 74: 228-230.
- PIANKA, E.R. 1970. On r- and k-selection. *Am. Nat.* 104: 592-197.
- POLLARD, E. 1979. Population ecology and change in range of the white admiral butterfly *Ladoga camilla* in England. *Ecol. Entomol.* 4: 61-74.
- RILEY, T.J. 1988. Effect of larval photoperiod on mating and reproductive diapause in seasonal forms of *Anaea andria* (Nymphalidae). *J. Lepid. Soc.* 42: 263-268.
- ROYAMA, T. 1981. Evaluation of mortality factors in insect life table analysis. *Ecol. Monographs* 51: 495-505.
- SOLOMON, M.E. 1964. Analysis of processes involved in the natural control of insects. *Adv. Ecol. Res.* 2: 1-58.
- SOUTHWOOD, T.R.E. 1978. *Ecological methods with particular reference to the study of insect populations*. Chapman and Hall, New York.
- STILING, P. 1988. Density-dependent processes and key factors in insect populations. *J. Anim. Ecol.* 57: 581-593.
- TILMAN, D. 1978. Cherries, ants and tent caterpillars: Timing of nectar production in relation to susceptibility of caterpillars to ant predation. *Ecology* 59: 686-692.
- WARREN, M.S., E. POLLARD & T.J. BIBBY. 1986. Annual and long-term changes in a population of the wood white butterfly *Leptidea sinapis*. *J. Anim. Ecol.* 55: 707-719.
- WINDSOR, D. M. 1990. Climate and moisture variability in a tropical forest: Long-

- term records from Barro Colorado Island, Panama. Smithsonian Institution Press, Washington, DC.
- WOLDA, H. 1983. "Long-term" stability of tropical insect populations. Res. Popul. Ecol. Suppl. 3: 112-126.
- 1989a. Seasonal cues in tropical organisms. Rainfall? Not necessarily! Oecologia 80: 437-442.
- 1989b. The equilibrium concept and density dependence tests. What does it all mean? Oecologia 81: 430-432.
- 1992a. Stability of environment and of insect populations. Res. Popul. Ecol. 34: 213-225.
- 1992b. Trends in abundance of tropical forest insects. Oecologia 89: 47-52.
- WOLDA, H. & R.W. FLOWERS. 1985. Seasonality and diversity of mayfly adults (Ephemeroptera) in a "nonseasonal" tropical environment. Biotropica 17: 330-335.
- WOLDA, H. & R. FOSTER. 1978. *Zunacetha annulata* (Lep.: Diptidae), an outbreak insect in a neotropical forest. Geo-Eco-Trop. 2: 443-454.